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The cormorants of Lake Ladoga in the early 20th century: Arctic invaders or continental colonists?

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There are two native subspecies of the great cormorant *Phalacrocorax carbo* in Europe: the mainly coastal nominate subspecies *carbo*, and the mainly continental subspecies *sinensis*. The population of the latter, in particular, has increased significantly in recent decades. Old literature records suggest that cormorants of some kind were breeding at the largest freshwater lake in Europe, Lake Ladoga, in the early part of the 20th century. A couple of specimens from this population were allegedly also collected; however, the current whereabouts of these specimens appear to be unknown. Recent studies have shown that both cormorant subspecies are ecologically fairly flexible and, therefore, breeding at a freshwater locality cannot by itself be regarded as evidence that they belonged to the continental subspecies *sinensis*. Thus, it is not possible to ascertain with certainty to which subspecies Lake Ladoga's cormorants belonged.

Introduction

The great cormorant *Phalacrocorax carbo* ('cormorant' from here on) is a species which, by its mere presence, often manages to evoke strong antipathy in humans. In particular, cormorants are accused of competing with fishermen, and mainly for this reason they have been heavily persecuted throughout recent history in Europe (Rusanen *et al*. 1998). This persecution has kept cormorant population numbers low in many European countries, or even eradicated this species from large parts of its range.

Following the introduction and enforcement of protective legislation in many countries, the recent decades have witnessed a remarkable population increase of cormorants in Europe, especially in the western and northern parts of the continent (e.g., Andersson *et al*. 1984, Hansen 1984, Van Eerden & Gregersen 1995, Rusanen *et al*. 1998, Engström 2001, Lehikoinen 2006, Herrmann *et al*. 2011). This has led to renewed human–cormorant conflicts, and even to suggestions that the current European cormorant populations are at least partly of non-native origin and have been augmented by deliberate introductions. These latter claims rest upon the idea that of the two currently recognized cormorant subspecies found in Europe, the Atlantic or the northern cormorant *Phalacrocorax carbo carbo* and the continental or the southern cormorant *Phalacrocorax carbo sinensis*, respectively, the latter is supposedly native to Asia rather than to Europe, and can therefore be eradicated as being a non-indigenous species. (Recently, Marion & Le Gentil (2006) suggested that there are actually three na-

tive European cormorant subspecies. According to these authors, the northernmost populations of *carbo* cormorants are genetically distinct enough to warrant recognition as a separate subspecies, *Phalacrocorax carbo norvegicus*. Here, however, the traditional taxonomy which recognises only two European cormorant subspecies is followed.)

Among modern ornithologists, there is no serious doubt that the *sinensis* cormorants are, in fact, native to Europe (e.g., Wirdheim 2009). Archaeological discoveries show that *sinensis*-like cormorants, which are distinguishable from *carbo* by their on average slightly smaller body size, are known from various regions in Europe, especially the eastern parts of the continent (Ericson & Hernández Carrasquilla 1997). On the other hand, in the northern parts of Europe such as the Baltic Sea region and the British Isles, osteological data suggest the prehistoric presence of cormorants belonging to the subspecies *carbo* (Ericson & Hernández Carrasquilla 1997, Stewart 2010). Partly on the basis of old eyewitness reports from the 17th and 18th centuries of supposedly *sinensis*-like cormorants in Sweden, it has been suggested (e.g., Engström 2001) that an actual replacement of cormorant subspecies has taken place in the Baltic Sea region within historical times, with *carbo* disappearing for unknown reasons and *sinensis* later invading and occupying its ecological niche. However, the lack of preserved physical specimens from the Baltic Sea region from the critical time period (from circa the year 1000 to 1800) makes such suggestions difficult to test, given the considerable overlap in physical and ecological characteristics between the two European cormorant subspecies (see below).

It is clear, however, that cormorants of some kind have been a part of the marine/coastal fauna of Fennoscandia for at least several millennia (cf. Mannermaa 2002, Mannermaa & Storå 2006), and, apparently, cormorants were also at least sporadically present at freshwater lakes in Sweden (Andersson *et al*. 1984, Engström 2001). By contrast, there appears to be no published records indicating the 'ancient' presence of cormorants at freshwater lakes in the northern and eastern parts of Fennoscandia. However, a few reports in the literature suggest that cormorants were, at least temporarily, breeding at Lake Ladoga in the early part of the 20th century.

The Lake Ladoga cormorants

With an area of over 18,000 km^2, Lake Ladoga is the largest freshwater lake in Europe (and, indeed, in the entire Western Palaearctic) (Subetto *et al*. 1998). Its separation from the Baltic Sea and its various pre-stages began approximately 10,000 YBP, during the Yoldia Sea stage, although connection with the pre-Baltic Sea was probably temporarily re-established at some point relatively shortly thereafter (Saarnisto 1970, Subetto *et al*. 1998). Lake Ladoga's large size and its open expanses give this freshwater body a somewhat 'marine' character, and this impression is accentuated by the fact that this lake's fauna includes a number of species which are obviously of marine origin. The best-known such example is Lake Ladoga's endemic, and morphologically distinct, ringed seal (Müller-Wille 1969, Hyvärinen & Nieminen 1990, Sipilä *et al*. 1996).

At the meeting of a Finnish scientific society, Societas pro Fauna et Flora Fennica, on December 3, 1910, a written communication by Walter Linnaniemi was read concerning the nesting of cormorants on the island of Kukri (or Kugri) (Anonymous 1911). This island, which is situated in the western parts of Lake Ladoga, was at that time administratively within Finnish territory; Finland, at that time, was not an independent nation, but an autonomous part of the Russian Empire. According to Linnaniemi's local informant, a Mr. Alopaeus, cormorants had bred on Kukri in the years 1909 and 1910. Linnaniemi's communication further stated that two cormorants (one adult and one subadult) had been collected and preserved as taxidermy specimens.

Prior to this report, there were no known nesting records of cormorants from anywhere within the geographical area of Finland (with the exception of the Petsamo area by the Arctic coast, which, however, was arguably not to be regarded as part of Finland proper). Admittedly, Itkonen (1915) had reported the discovery of a presumed cormorant's nest with three eggs from the Finnish side of the northern part of the Gulf of Bothnia, at the Kemi River estuary, in 1913. However, no further evidence for this claim was presented and Hortling (1922) therefore regarded this case as dubious. Linnaniemi's report of breeding cormorants at Lake Ladoga was thus of considerable

Fig. 1. Rolf Palmgren (1880–1944).

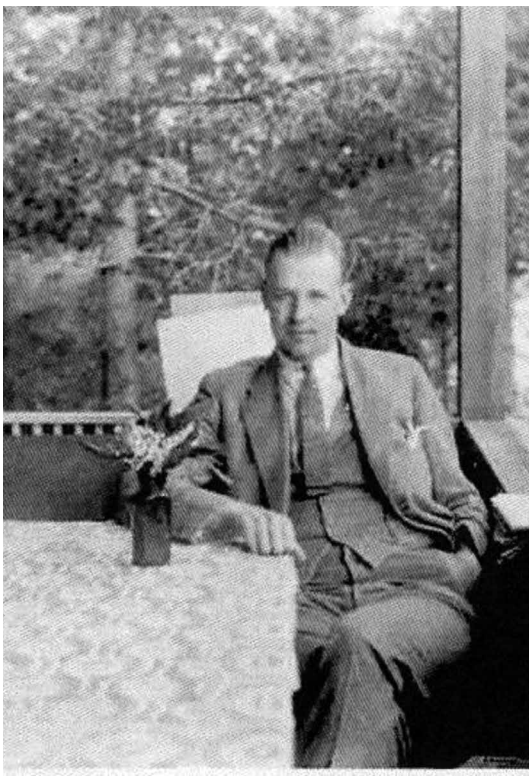

Fig. 2. Ilmari Hildén (1899–1963). Photo courtesy of Maarit Roos.

faunistic interest, but it did not lead, at least not immediately, to any notable discussion in the scientific literature either within or outside of Finland.

In the spring of 1916, the ornithologist Rolf Palmgren (Fig. 1) 'glanced' through the published proceedings of the Societas pro Fauna et Flora Fennica meeting of December 3, 1910, and noticed the report on the Lake Ladoga cormorants (Palmgren 1917:9). This raised his interest in the subject to the extent that he decided to investigate the matter for himself, and thus he visited Lake Ladoga in June 1916 (Palmgren 1917). At the time of Palmgren's visit, however, no cormorants were breeding on Kukri. Palmgren's local informants told him that, following the previous harsh winter, the cormorants had not attempted to breed there that year. Palmgren did, however, consider Linnaniemi's and the locals' earlier accounts to be reliable and concluded that the cormorant was now a member of the breeding bird fauna of Finland. Palmgren also reported that he had been shown the two collected cormorant specimens mentioned by Linnaniemi.

In 1917, the year after Palmgren's visit to Lake Ladoga, Finland gained her independence from Russia/the Soviet Republic. The Fenno-Soviet border was drawn across Lake Ladoga so that the western parts of the lake remained as Finnish territory. As a consequence of Lake Ladoga's new strategic importance as a national border zone, the Finnish military begun to fortify several of its islands. This activity was noted by the young ornithologist Ilmari Hildén (Fig. 2), who visited Lake Ladoga in June 1920 (Hildén 1921a, b). According to Hildén, who was aware of Palmgren's paper on the Lake Ladoga cormorants, the cormorants were that year breeding on the island of Vossina (or Vossinoi). Hildén (1921a, b) also predicted that the fortification work carried out by the military on Vossina and other nearby islands might disturb the cormorants so much that they would abandon their nesting sites. Lake Ladoga's small cormorant colony does indeed seem to have been negatively affected by the increased human presence (and possible persecution); in any case, after 1921 there are very few published reports of the presence of breeding cormorants at Lake Ladoga. Räsänen (1928) and Pankakoski (1941) published observations that, in these authors'

opinions, suggested breeding at the lake in the years 1928 and 1939, respectively, but neither author claimed to have seen unambiguous evidence of nesting. In a listing of Lake Ladoga's avifauna, however, Paatela (1947) stated that cormorants had definitely returned to nest on the island of Kukri in 1924, where a juvenile bird was allegedly shot that year.

It appears that by the 1940ies and onwards, cormorants were no longer breeding at Lake Ladoga. To this author's knowledge, Paatela's (1947) paper was the last published original literature reference to cormorants breeding at this lake, at least in non-Slavic languages. After the Second World War, the Fenno-Soviet border was redrawn, and since then Lake Ladoga in its entirety was within Soviet (now Russian) territory, which significantly restricted access of Finnish and other Western ornithologists to it. After the fall of the Soviet Union in the 1990ies, Finnish ornithologists were again able to visit Lake Ladoga. However, by then there were no longer any indications of breeding by cormorants at the lake (Pakarinen & Siikavirta 1993, Peiponen & Kolunen 1993).

The extent of morphological and ecological overlap between *carbo* and *sinensis*

To which subspecies did the Lake Ladoga cormorants belong? Palmgren (1917) did not consider this question to be particularly important, and only went so far as to suggest that the Lake Ladoga cormorants might have originally spread to the lake from the Arctic coast. In this case, they would presumably belong to the subspecies *carbo*. However, Palmgren considered the cormorant to be so ecologically and behaviourally adaptable that breeding sites and localities were of little or no use as indicators of subspecific allocation.

Modern scientific methods have brought new insights into the question of subspecific differentiation of the European cormorants. Comparisons of the molecular structure of hypervariable microsatellite markers in *carbo* and *sinensis* cormorants from Europe suggest that these two subspecies are approximately as distinct from each other as is the carrion crow *Corvus corone corone* from the hooded crow *Corvus corone cornix* (Goostrey *et al*. 1998). These two crows have usually been considered only subspecifically distinct, but nowadays they are increasingly often treated as full species (e.g., by the British Ornithologists' Union; see Knox *et al*. 2002). There are, of course, currently no universally accepted criteria for how to delimit subspecies from full species; such criteria differ according to which of the several existing species concepts one follows. According to the Biological Species Concept, for example, the fact that carrion and hooded crows do hybridise in nature means that they might best be considered subspecies of the same species. On the other hand, according to the Phylogenetic Species Concept, the fact that carrion and hooded crows are genetically distinct evolutionary lineages that also remain diagnosably distinct in spite of occasional gene flow through hybridisation means that they may be considered full species. In other words, whether to consider *carbo* and *sinensis* to be subspecies of the same species or full species in their own right depends on which species concept one chooses; there is no 'correct' answer. (The literature on different species concepts is substantial and a review is beyond the scope of this paper. For discussion on species concepts specifically from an ornithological perspective, see Cracraft 1983, McKitrick & Zink 1988, Zink & McKitrick 1995, Helbig *et al*. 2002).

In the field, *carbo* and *sinensis* cormorants can be distinguished from each other only with difficulty, or not at all. Although *carbo* is on average slightly larger and more robust (e.g., Lönnberg 1915, Cramp 1977, Alström 1985), this size difference is rarely obvious in the field and, furthermore, there is also some size overlap between these two subspecies (Millington 2005, Newson *et al*. 2005). The plumage of *sinensis* cormorants is usually greenish, rather than purplish as in *carbo* cormorants (but see Stokoe 1958), and *sinensis* cormorants often have more white feathers on their heads during the breeding season than *carbo* cormorants do. However, these plumage differences are highly variable and therefore by themselves unreliable as subspecific indicators (Stokoe 1958, Marion 1983, Ekins 1997, Millington 2005, Newson *et al*. 2005).

Alström (1985) suggested that the shape of the gular pouch is a reliable indicator of subspe-

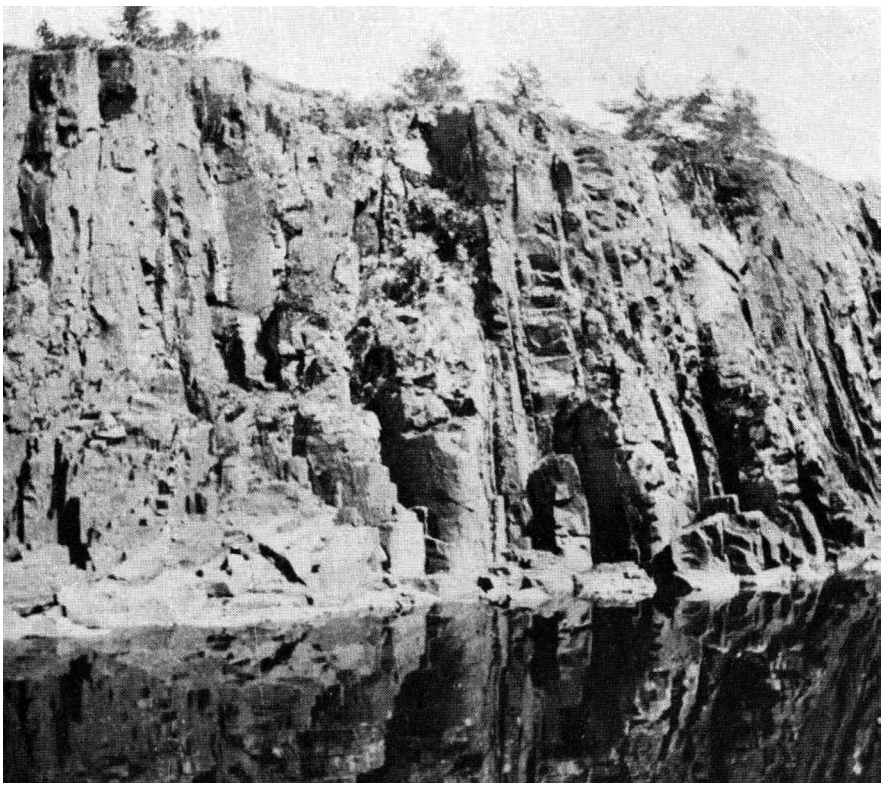

Fig. 3. The former nesting site on the island of Kukri in 1916. Photo: Rolf Palmgren.

cific identity in cormorants. In *carbo*, its angle relative to the bill is less than 60° whereas in *sinensis*, its angle relative to the bill is nearly 90°. Some authors (e.g., Marion 1995) have doubted the usefulness of this morphological criterion for separating the subspecies; however, later quantitative studies (Newson *et al*. 2004, 2005) have shown that gular pouch angle measurement is indeed a fairly reliable way to differentiate between cormorants of different subspecies (although individuals of hybrid origin might potentially pose challenges).

Traditionally, the *carbo* and the *sinensis* cormorants have been thought to be quite strictly separated ecologically, with the former breeding in marine and the latter in freshwater habitats, sometimes at a considerable distance from the sea. However, to an increasing extent, both subspecies nowadays meet and intermingle in the same wintering ground habitats in Western Europe (Marion 1983, 1995, Fonteneau *et al*. 2009). Furthermore, in recent years, cormorants of the subspecies *carbo* have also started to breed at inland localities by freshwater, in both Britain and France (Sellers 1993, Ekins 1997, Goostrey et al. 1998, Winney *et al*. 2001, Carss & Ekins 2002, Marion & Le Gentil 2006, Newson *et al*. 2006, 2007). In such areas where the two subspecies mix in the breeding season, hybridisation between them is presumed to occur (Sellers *et al*. 1997, Goostrey *et al*. 1998, Winney *et al*. 2001, Carss & Ekins 2002, Marion & Le Gentil 2006).

Breeding site characteristics have also been thought to segregate Atlantic and continental cormorants, with the former preferring steep cliff sides, and the latter relatively flat ground or, especially, trees. Palmgren (1917) noted that the breeding sites of the cormorants on the island of Kukri were steep cliff sides reminiscent of those by the Arctic coast where cormorants (of the subspecies *carbo*) traditionally breed (Fig. 3). It was mainly on the basis of this observation that he tentatively suggested (whilst, as mentioned, not considering the subspecies question to be of any great importance) that Lake Ladoga's cormorants might be of Arctic origin. However, as has been documented since, the two cormorants are less strictly separated regarding their nest site prefer-

Fig. 4. Cormorant; avian specimen No. 9799 in the collections of the Finnish Museum of Natural History, Helsinki. This female, which most likely belongs to the subspecies *sinensis*, was collected at Lake Ladoga on October 23, 1928 (i.e., well after the cormorants' breeding season). Photo: Janne Granroth.

ences than has usually been presumed. In the UK, the *carbo* cormorants that nest in inland colonies together with *sinensis* cormorants have adapted the latters' breeding habits and frequently nest in trees (Sellers 1993, Ekins 1997, Sellers *et al*. 1997, Carss & Ekins 2002, Newson *et al*. 2006, 2007). On the other hand, in the Baltic Sea region, *sinensis* cormorants nowadays often nest on treeless rocky islands in a marine/brackish habitat (Lehikoinen 2006).

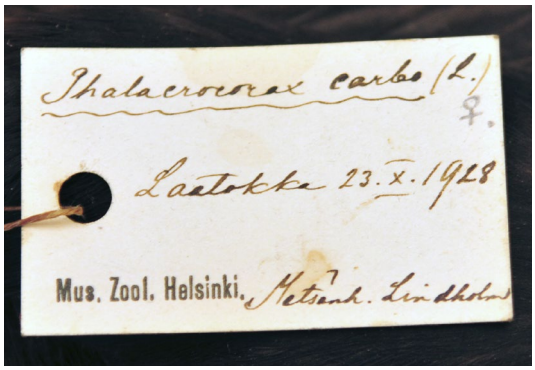

Fig. 5. Close-up of the museum label of specimen 9799. The text (in Finnish) says: "Phalacrocorax carbo (L.) ♀. [Lake] Ladoga 23. X 1928. Mus. Zool. Helsinki. Forester Lindholm". Photo: Janne Granroth.

The missing puzzle pieces: the cormorant specimens collected from Lake Ladoga

As mentioned by Anonymous (1911) and confirmed by Palmgren (1917), at least two cormorants from Lake Ladoga's breeding population were collected and mounted. The current whereabouts of these specimens appear to be unknown. They are not housed in the largest zoological collections in Finland, those of the Finnish Museum of Natural History in Helsinki (pers. obs. and J. Granroth pers. comm.). These collections do include one female cormorant from Lake Ladoga (Figs. 4–5), but as this individual was collected in 1928 it obviously cannot be one of those that Palmgren referred to. Furthermore, as this bird was collected outside of the cormorants' breeding season its presence at Lake Ladoga need not indicate residency; it may have been a vagrant. The large gular pouch angle of this specimen suggests that it belongs to the subspecies *sinensis* (Alström 1985, Newson *et al*. 2004, 2005). The dimensions of the bill, tarsus, and tail are also consistent with those of a female *sinensis* (Table 1).

These Lake Ladoga cormorant specimens apparently have not ended up in other major natural history collections in Finland either. E-mail enquiries by the author (September 2013) revealed that they are not housed in the Turku Natural History Museum (A. Karhilahti pers. comm.), the Zoological Museum in Oulu (J. Aspi pers. comm.), the Kuopio Natural History Museum (P. Renvall pers. comm.), or the Natural History Museum in Jyväskylä (J. Mäntynen pers. comm.). These specimens have also not ended up in the Zoological Institute of the Russian Academy of Sciences, St. Petersburg (V. Vysotsky pers. comm.), or in the Darwin Museum in Moscow (I. Fadeev pers. comm.). There is a slight chance that they have

Table 1. Selected measurements of cormorant specimen No. 9799 in the collections of the Finnish Museum of Natural History, Helsinki, compared with those of adult *carbo* and *sinensis* females (averages and ranges in parentheses), following Cramp (1977). Bill depth is the lowest depth of the bill in the middle. Measurements are in millimeters.

	carbo	*sinensis*	9799
tail length	150 (135–163)	144 (133–154)	150
bill length	63.7 (59–68)	55.7 (50–58)	57.8
bill depth	14.1 (13–15)	11.8 (11–13)	12.8
tarsus length	70.6 (67–74)	66.1 (64–70)	66.4

been preserved in some private collection, perhaps in the formerly Finnish, nowadays Russian, town of Sortavala/Сóртавала, where they were at least initially stored (Anonymous 1911). However, on current evidence it seems that these mounted Lake Ladoga cormorant specimens are, regrettably, lost to science.

As physical specimens and/or illustrations of them are lacking, there is no reliable way to determine the subspecific identity of the cormorants breeding at Lake Ladoga in the early part of the 20th century. Pending further evidence, they must therefore be considered as undetermined in this regard.

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